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Matters

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Abstract

Enveloped viruses fuse with host membranes without affecting cell integrity. Non-enveloped viruses and bacteria penetrate by rupturing endosomal membranes, and thereby expose complex-type carbohydrates from the endosome lumen to cytosolic proteins. Here we report on the dynamics and initial marker analyses of Galectin-3 (Gal3)-positive membranes triggered by incoming adenovirus species B/C in HeLa cells. Using mCherry-Gal3 reporter constructs, immuno-labeling, confocal and electron microscopy, we detected robust signals from Gal3-containing, early endosomal antigen 1-positive membranes 1h post-infection (pi). Adenoviruses penetrate from non-acidic endosomes with high efficiency, 15min pi, and largely outnumbered the Gal3-positive membranes, suggesting that Gal3 recruitment to broken membranes is transient, or Gal3-positive membranes are rapidly turned-over. In support of rapid turn-over, Gal3 was found within single membrane vesicles and degradative autophagosomes. The Gal3-membranes

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Figure

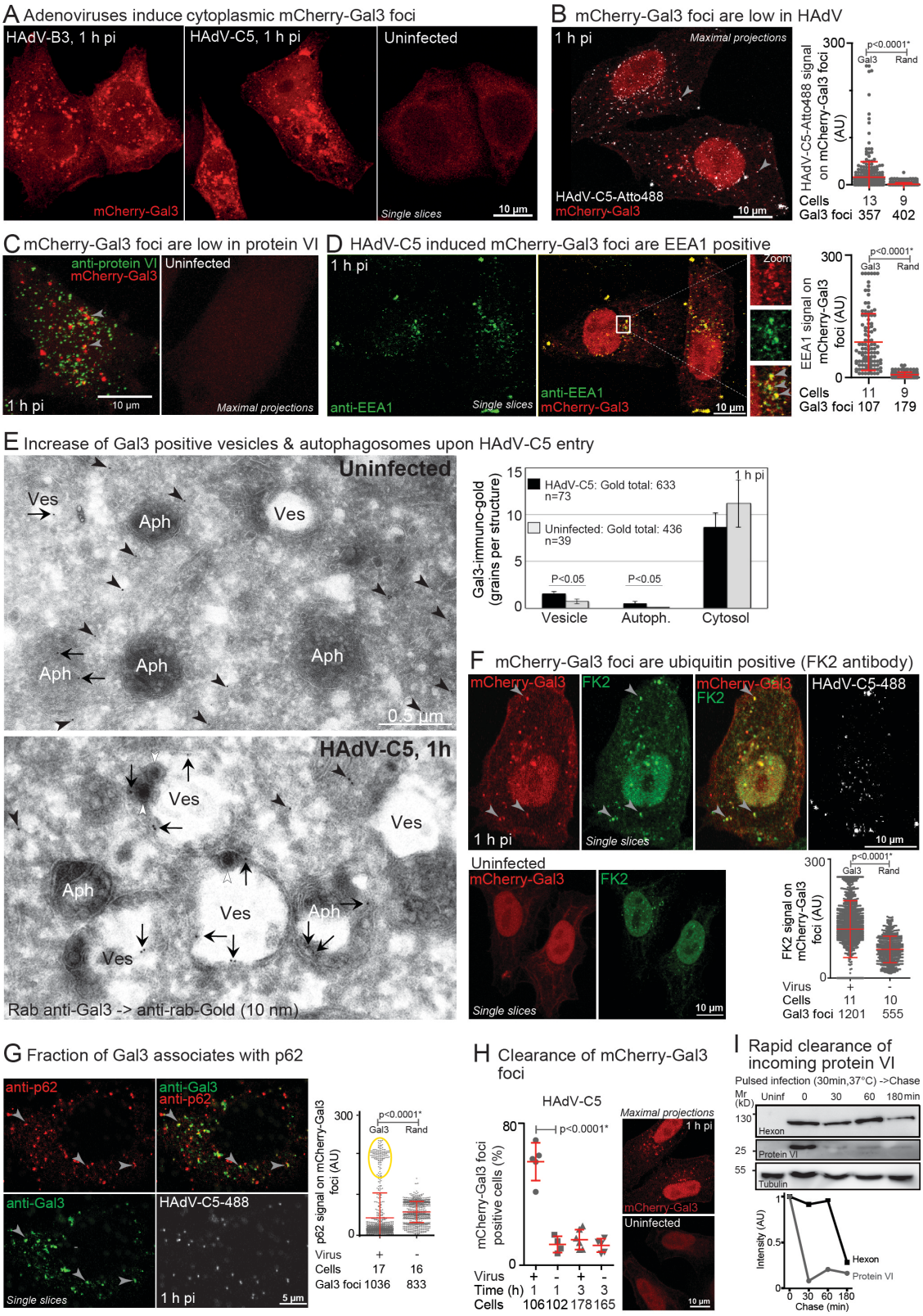
A Adenoviruses induce cytoplasmic mCherry-Gal3 foci
HAdV-B3, 1 h pi
HAdV-C5, 1 h pi
Uninfected
mCherry-Gal3
Single slices
10 µm
B mCherry-Gal3 foci are low in HAdV
1 h pi
Maximal projections
HAdV-C5-Atto488
mCherry-Gal3
10 µm
HAdV-C5-Atto488 signal on mCherry-Gal3 foci (AU)
p<0.0001*
Gal3
Rand
300
0
Cells 13 9
Gal3 foci 357 402
C mCherry-Gal3 foci are low in protein VI
anti-protein VI
mCherry-Gal3
Uninfected
1 h pi
10 µm
Maximal projections
D HAdV-C5 induced mCherry-Gal3 foci are EEA1 positive
1 h pi
anti-EEA1
Single slices
anti-EEA1
mCherry-Gal3
10 µm
Zoom
EEA1 signal on mCherry-Gal3 foci (AU)
Cells 11 9
Gal3 foci 107 179
E Increase of Gal3 positive vesicles & autophagosomes upon HAdV-C5 entry
Uninfected
Ves
Aph
0.5 µm
HAdV-C5, 1h
Rab anti-Gal3 -> anti-rab-Gold (10 nm)
Gal3-immuno-gold (grains per structure)
HAdV-C5: Gold total: 633
n=73
Uninfected: Gold total: 436
n=39
1 h pi
P<0.05
Vesicle
Autoph.
Cytosol
F mCherry-Gal3 foci are ubiquitin positive (FK2 antibody)
mCherry-Gal3
FK2
HAdV-C5-488
1 h pi
Single slices
10 µm
Uninfected
FK2 signal on mCherry-Gal3 foci (AU)
Virus + -
Cells 11 10
Gal3 foci 1201 555
G Fraction of Gal3 associates with p62
anti-p62
anti-Gal3
HAdV-C5-488
Single slices
1 h pi
5 µm
p62 signal on mCherry-Gal3 foci (AU)
Virus + -
Cells 17 16
Gal3 foci 1036 833
H Clearance of mCherry-Gal3 foci
HAdV-C5
mCherry-Gal3 foci positive cells (%)
Virus + - + -
Time (h) 1 1 3 3
Cells 106 102 178 165
Maximal projections
1 h pi
mCherry-Gal3
Uninfected
I Rapid clearance of incoming protein VI
Pulsed infection (30min,37°C) ->Chase
Mr (kD)
Uninf 0 30 60 180 min
130
25
55
Hexon
Protein VI
Tubulin
Intensity (AU)
Chase (min)

Figure 1: The nature of adenovirus ruptured Gal3-positive endosomes.
A) Infection of HeLa cells with HAdV-B3 or HAdV-C5 for 1h induces the formation of cytoplasmic Gal3 foci. Results show single optical sections from confocal laser scanning fluorescence microscopy.
B) Gal3 foci are low in HAdV-C5 particles. HeLa cells expressing mCherry-Gal3 were infected with HAdV-C5-Alexa488 at 37°C for 1h, fixed and analyzed for virus co-localization with cytoplasmic mCherry-Gal3 foci using maximal projections of confocal fluorescence microscopy slices from the entire cell. Note that in order to detect good mCherry-Gal3 foci, dozens of virus particles were required per cell. The number and intensity of the Gal3 foci was dependent on the expression levels of mCherry-Gal3 in the cell, and correlated with variable amounts of red fluorescence in the nucleus, presumably from cytosolic mCherry-Gal3. For image quantification, an average size of the Gal3 foci was defined by a computational mask, and used to determine the signal intensity of HAdV-C5-Alexa488 in the Gal3 foci (Gal3, left column of the dot plot). To estimate background co-localization signals, HAdV-C5-Alexa488 fluorescence was determined in randomly placed masks across the cytoplasm (Rand, right column). Each dot represents the signal from one mask. Number of cells and Gal3 foci analyzed are indicated. Mean values with standard deviation (SD) are shown in red. Note that only a small amount of Gal3 foci was positive for virus.
C) mCherry-Gal3 foci are low in protein VI from incoming HAdV-C2. Arrows in this representative cell denote co-localization events of mCherry-Gal3 and protein VI observed in single section confocal slices (not shown). Shown here are maximal projections of the signals to give an overall impression.
D) Gal3 foci are positive for early endosome antigen 1 (EEA1). Results were analyzed as described in panels A and B from Gal3 foci and cells as indicated. Results show a significant enrichment of EEA1 on mCherry-Gal3 foci. Mean values with SD are shown in red.
E) HAdV-C5 entry enhances the vesicular and autophagosomal levels of Gal3. Cells were infected with HAdV-C5 at 37°C for 1h, fixed and processed for cryo-immuno labeling as described. Ultrathin cryo-sections were stained with rabbit anti-Gal3 antibodies followed by protein A conjugated to 10nm colloidal gold, and analysis by electron microscopy in a Philips CM100 (100kV at 46000 magnification). Gold particles were manually counted in vesicles (Ves), autophagosomes (Aph) and the cytosol. Arrows indicate gold in vesicles or autophagosomes, black arrow heads cytosolic gold, and white arrow heads endosomal HAdV-C5 particles. Autophagosomes were identified as structures containing electron-dense material and a closely apposed double membrane at least partially visible in the sections, as suggested in the guidelines from the autophagy community **[1]**. Mean number of gold particles per structure, and p-values (Student's t-test) were derived from indicated number of vesicles, autophagosomes, and gold particle. Gold in the cytosol was analyzed in the same images as for vesicle and autophagosome analyses. Note the trend to reduced cytosolic Gal3 pools in HAdV-C5 infected cells. Note that 13 from 22 autophagosomes of infected cells contained Gal3, compared to 1 from 10 Gal3 positive autophagosomes of uninfected cells, indicating a strong enhancement of Gal3 positive autophagomes upon HAdV-C5 infection.

F) mCherry-Gal3 foci contain epitopes for the pan-ubiquitin antibody FK2. Images were acquired and analyzed as described above. Mean values with SD are shown in red.
G) A fraction of the Gal3 foci induced by HAdV-C5 is positive for the poly-ubiquitin binding protein p62/sequestosome 1 (p62/SQSTM1). Analyses indicate that about 10% of the Gal3 foci contain the poly-ubiquitin binding protein p62/SQSTM1 (yellow ellipse), while the rest is indistinguishable from the random control, indicated by means and SD values.
H) HAdV-C5 induced mCherry-Gal3 foci are rapidly cleared from infected cells. Cells were infected at 37°C for 1h, washed free of virus, and analyzed directly (1h time point), or after 2h incubation at 37°C in fresh medium (3h time point). The percentage of cells showing mCherry-Gal3 foci was plotted. One dot represents the fraction of positive cells per image. Shown are the mean values with SD, and the total number of cells analyzed per sample with p-values from unpaired t-tests.
I) The membrane-lytic protein VI from incoming HAdV-C5 is rapidly cleared from infected cells. HAdV-C5 particles were allowed to bind and internalize into HeLa cells at 37°C for 30min, after which unbound virus was removed and cells were further incubated at 37°C for the indicated times. Amounts of protein VI and the major capsid protein hexon in cell extracts were determined by SDS-PAGE and Western blotting using β-tubulin as a loading control. Densitometric analyses of protein bands normalized to tubulin are shown as OD values relative to the 0min time point.
Raw data and statistical analyses can be found in the supplementary excel sheet.

Introduction

All viruses and many bacteria that enter eukaryotic cells activate a genetic program for replication and immune evasion [2] [3] [4]. Invariably, host defense against the pathogens or host cell damage antagonizes the intruders [5] [6] [7]. Damage to host cells occurs during invasion of bacteria and non-enveloped viruses, including *Salmonella*, *Shigella*, *Listeria* or Adenovirus, which disrupt phagocytic vacuoles and endosomes [8] [9]. Disrupted vacuoles recruit beta-galactoside binding lectins, such as galectin-3 (Gal3) and Gal8, both widely expressed in epithelial cells [10] [11] [12] [13]. Cytosolic galectins can also be subject to export by leader peptide-independent mechanisms [14] [15] [16]. They can bind to enveloped viruses and bacteria, and act as pattern recognition receptors [17]. Intracellular Gal8 coordinates the destruction of disrupted late endosomes and associated bacteria by autophagy, whereas Gal3 is involved in membrane sorting by clustering glycoproteins and glycolipids, and modulation of cell-cell contacts during organogenesis [18] [19] [20].

Recently, Gal3 was reported to be recruited to endosomes disrupted by incoming human adenovirus type 5 (HAdV-C5) [13] [21]. Adenoviruses are non-enveloped human pathogens and widely used vectors in clinical gene therapy and vaccination [22] [23] [24] [25]. HAdV-C2 and C5 enter epithelial cells by receptor-mediated endocytosis and a stepwise uncoating program initiated at the plasma membrane by the differential movements of two receptors, integrin and coxsackievirus adenovirus receptor (CAR) [26] [27] [28]. Virus penetration into the cytosol occurs from early endosomes in a pH-independent manner [29] [30]. It requires the membrane-lytic viral protein VI [31] [32] [33], lysosomal secretion, the sphingolipid ceramide [34] [35], and gates the pathway for viral DNA genome separation from the capsid and nuclear delivery of the viral genome [36] [37]. Here, we describe a novel observation, the recruitment of Gal3, ubiquitin and the poly-ubiquitin binding protein p62/SQSTM1 to ruptured early endosomes, followed by clearance of disrupted membranes without clearance of virus particles from the infected cell. p62/SQSTM1 is an adaptor linking poly-ubiquitination to macroautophagy [38] [39]. We speculate that this mode of clearance is pro-viral, in contrast to the recruitment of Gal8 to ruptured phagosomal vacuoles in *Salmonella* infected cells, which presents a mode of pathogen restriction [12].

Objective

Ruptured host membranes are danger signals, and enhance innate immunity against infections. The objective here was to analyze the composition and dynamics of ruptured endosomes induced upon virus entry into cells.

Results & Discussion

Most viruses engage in receptor-mediated endocytosis and extensive membrane trafficking

using cellular mechanisms [40] [41]. Enveloped viruses encode membrane proteins, which fuse the viral and endosomal membranes, or, in rare cases, the plasma membrane. Non-enveloped viruses are membrane-free, except for certain picornaviruses which occur in both enveloped and non-enveloped forms [42]. They all encode membrane-interacting proteins, which are typically encased in a capsid, and can be activated or exposed by cues from the host cell during entry [35] [43]. Activation of membrane-active proteins leads to pore formation, piercing or rupture of the host membrane [44] [45] [46]. Rupture of internal membranes by HAdV-C5 exposes sugar epitopes to cytosolic proteins, and recruits cytosolic Gal3 to the broken membranes [13].

To track broken membranes, we expressed mCherry-Gal3 fusion protein in HeLa cells, followed by continuous infection with HAdV-C5 or HAdV-B3 for 1h. HAdV-C5 enters epithelial cells through CAR and integrin receptors, and HAdV-B3 through CD46 and desmoglein-2 receptors [3] [47] [48] [49]. Both viruses penetrate HeLa cells independent of endosomal acidification with an efficiency higher than 70% (HAdV-C5) or about 40% (HAdV-B3) within 30min of cold-synchronized infection [30]. Uninfected cells had diffuse cytoplasmic red fluorescence and variable levels of nuclear red fluorescence, in contrast to the prominent cytoplasmic mCherry-Gal3 foci in both types of infected cells, indicating that membrane rupture was independent of the nature of entry receptors (Fig. 1A, and for additional uninfected cells, see panels 1C, F, H). Most of the mCherry-Gal3 foci were devoid of HAdV-C5 particles labeled with Alexa488 fluorophore, as indicated by quantitative image analyses of single confocal slices (Fig. 1B, shown are maximal projections of confocal stacked images). Note that only two of the overlapping puncta co-localized in any of the single confocal slices (indicated by grey arrow heads; single slices not shown). Poor co-localization of HAdV-C2 and mCherry-Gal3 foci was confirmed by a low overlap of mCherry-Gal3 with the incoming membrane lytic viral protein VI, detected by an affinity-purified polyclonal antibody (Fig. 1C, two arrow heads point to the only co-localization events in these cells by single slice analyses). In contrast, a large fraction of the mCherry-Gal3 foci was robustly positive for the early endosomal antigen 1 (EEA1), indicating that the broken membranes had features of early endosomes (Fig. 1D). These results were in agreement with earlier notions that HAdV escapes quickly from endosomes and is transported by dynein/dynactin mediated processes towards the nucleus [50] [51] [52]. Protein VI on the other hand likely remains membrane associated, and may be sorted separately for degradation [26] [53].

Remarkably, visual inspection of the images suggested that the number of HAdV-C5 particles, or protein VI puncta exceeded the number of mCherry-Gal3 foci (Fig. 1B,C). The same observation was made with HAdV-B3 infected cells (not shown). Although the resolution of virus structures and Gal3-positive membranes was diffraction-limited in our confocal micrographs, the number of mCherry-Gal3 foci correlated with virus dose (data not shown). We also noted that Gal3 foci robustly emerged with 1h continuous infection schemes, but were rarely visible with shorter infection pulses or at 20min post-warming after cold-synchronized infections (data not shown). Since virus penetration from endosomes is asynchronous, and may involve different types of endosomes (clathrin-derived endosomes and macropinosomes), but not late endosomes and lysosomes [29],

we tested if Gal3-positive membranes were turned-over. Ultrastructural analyses of Gal3 by immuno-electron microscopy in cryo-sections of normal HeLa cells (not transfected with mCherry-Gal3 constructs) showed that most Gal3 immuno-gold signal was in the cytosol, as expected, although infected cells tended to have less cytosolic Gal3 than uninfected cells (Fig. 1E). Infected cells, however, had more Gal3 within vesicles and autophagosomes than uninfected cells. We tentatively classified the Gal3-positive autophagosomes as degradative autophagosomes, based on their partly visible double bilayer membranes, and contents comprising electron-dense organelle-like material [1] (Fig. 1E, structures labeled Aph). The structures described here are different from amphisomes, which are formed when an endosome fuses with an autophagosome [1]. Our Gal3-positive autophagosomes appear to contain internal membrane remnants (Fig. 1E), and are cleared with faster kinetics than calcium phosphate damaged endosomes, and silica- or LLOMe-damaged lysosomes, which are cleared by amphisomes [54] [55].

Further immuno-fluorescence microscopy analyses indicated that the HAdV-C5 induced mCherry-Gal3 foci were strongly positive for the pan-ubiquitin antibody FK2 (Fig. 1F), and a fraction of these foci was positive for the poly-ubiquitin binding protein p62/SQSTM1 (Fig. 1G). Interestingly, the autophagic marker LC3B was not enriched on mCherry-Gal3 or EEA1 positive membranes of infected cells, but remained diffuse in the cytoplasm (data not shown). This suggested that ubiquitin coordinates LC3B-independent steps for recruiting the autophagic machinery to clear the broken early endosomes. In agreement with this notion, we found that the mCherry-Gal3 foci were readily cleared from the infected cells within 3h of infection (Fig. 1H). The clearance kinetics of the broken early endosomes was considerably slower than the disappearance of protein VI, which was nearly undetectable in Western blots 30min pi (Fig. 1I).

In sum, the data are reminiscent of a previous observation that ruptured phagocytic vacuoles in *Shigella* infected cells are poly-ubiquitinated, p62/SQSTM1 positive and targeted for autophagic destruction, with concomitant reduction of early inflammatory and cytokine responses [10]. Our data support the earlier finding that the levels of Gal3 and p62/SQSTM1 are reduced in HAdV-B3 or C5 infected A549 human epithelial cells compared to uninfected cells [56]. We suggest the term ‘endosomophagy’ for the clearance of broken early endosomes, and speculate that endosomophagy suppresses danger signals and cell death pathways, and enhances virus infection. This is distinct from lysophagy, which can be induced by chemicals, such as the lysosomotropic reagent L-Leucyl-L-leucine methyl ester (LLOMe), which oligomerizes, forms toxic products in the lysosomal lumen, leads to lysosomal lysis, and thereby triggers necrosis [57] [58] [59].

Conclusions

The observation here shows that adenovirus ruptured early endosomal membranes are targeted for clearance. These membranes are Gal3-positive, contain ubiquitin and the polyubiquitin-binding protein p62/SQSTM1, and are associated with degradative autophagosomes. This endosomal clearance is termed here 'endosomophagy'. It is distinct from lysosomal rupture, which leads to inflammation and necrotic cell death.

Conjectures

Our observation has implications for innate immunity, inflammation, and infectious disease. Notably, in spite of the robust cross-reacting cellular and humoral immune responses against HAdV infections, latent or persistent adenovirus infections in humans occur, and may last for years [60]. The report here also impinges on gene therapy and vaccination protocols, considering the prominent roles of adenoviruses in clinical gene therapy, and as vaccination adjuvants [61]. Follow-up analyses of this observation can be directed to the identification of host and viral targets for ubiquitin ligases and deubiquitinases, host adaptor proteins, or the role of virus induced-sphingolipids in tuning endosomophagy [34]. Notably, sphingolipids have key roles in the regulation of autophagy at the levels of transcription, translation and morphogenesis of autophagosomes [62]. Another emerging question is how Gal3 and ubiquitin turnover are orchestrated on the ruptured membranes. Further studies can also be directed towards professional antigen-presenting cells, such as macrophages and dendritic cells, which play a major role in inducing and controlling local and global immune responses [63]. Finally, specific experiments can address the question if the clearance of the membrane-lytic viral protein VI is related to or distinct from the mechanism of endosomophagy.

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Ethics statement

Not applicable

No fraudulence is committed in performing these experiments or during processing of the data. We understand that in the case of fraudulence, the study can be retracted by Matters.

Methods

Cells and viruses
HeLa cervical carcinoma cells, subline Ohio (from L. Kaiser, University Hospital, Geneva, Switzerland), were grown at 37°C under 5% CO2 in Dulbecco's modified Eagle's medium (DMEM; Sigma) supplemented with 7.5% fetal calf serum (FCS; Life Technologies) and 1% nonessential amino acids (Sigma). HAdV-C2, HAdV-C5 and HAdV-B3 were grown in human bronchial epithelial A549 cells (American Type Culture Collection), isolated, and labeled with Alexa Fluor 488 (Alexa488; Life Technologies) as previously described [30].

Immunofluorescence analysis of Gal3 foci
The pmCherry-Gal3 construct was generated by PCR amplification of Gal3 coding sequence from U2OS cDNA flanked by HindIII and EcoRI sites and cloned into pmCherry-C1 (Clontech). HeLa Ohio cells (0.5x106) were transfected with 8μg of pmCherry-Gal3 using Neon technology (100μl tip, 1005V, 35ms, 2 pulses; Life Technologies). Cells expressing Gal3 with an N-terminal mCherry tag (mCherry-Gal3) were grown in 24-well glass coverslips for 24h then exposed to continuous infection with 1-5μg/ml virus for the indicated time points. Cells were subsequently fixed in 4% PFA and stained with an anti-EEA1 antibody (mouse, clone 14; Transduction Laboratories), anti-p62/SQSTM1 antibody (mouse, clone 5F2; MBL) or the anti-ubiquitin antibody FK2 (Life Sensors) that detects K29-, K48-, and K63-linked mono- and poly-ubiquitinated proteins.
Imaging was performed with a Leica SP5 confocal microscope equipped with a 40× objective (oil immersion, numerical aperture 1.25) and a 63x objective (oil immersion, numerical aperture 1.25). Z-stacks composed of 8x0.5 µm steps were acquired at a frequency of 8000 Hz applying bidirectional scan, line averaging 32x and minimized acquisition time. Maximum projections of Z-stacks were analyzed using a customized Matlab routine (Matlab 2009b, available upon request). Fluorescence intensity of either virus labeling or antibody staining on the position of mCherry-Gal3 foci was determined and mean values per cell are shown. To evaluate background values in uninfected cells without mCherry-Gal3 foci, randomly generated and cytosolic foci of pixel size equivalent to mCherry-Gal3 foci localized were quantified. Further details are described in [30] [26].
Statistical analyses were performed using GraphPad Prism software (Version 5, GraphPad Software, Inc. La Jolla). Single-cell-based assays are represented as scatter dot plots, where the horizontal bars indicate the mean value and the vertical bars the standard

deviation. Two-tailed P-values were calculated by unpaired t-tests with Welch's correction and confidence interval 95%.

Co-localization of mCherry-Gal3 and protein VI

pmCherry-Gal3-transfected HeLa-Ohio cells grown on coverslips in 24-well dish were infected with 0.8μg atto647-labeled HAdV-C2 (kindly provided by I-Hsuan Wang) for 1h at 37°C. Control cells did not receive any virus. Cells were stained with affinity-purified rabbit anti-protein VI antibodies [26] and secondary AlexaFluor 488-conjugated anti-rabbit antibodies. Samples were imaged with Leica SP5 confocal laser scanning microscope using a 63× objective (oil immersion, numerical aperture 1.4) and zoom factor 4. Stacks were recorded at 0.5-μm intervals using 4× averaging, between frames sequential method and a frequency of 1000Hz. Shown are maximal projections of Z-stacks, but co-localization of protein VI and mCherry-Gal3 dots were checked also on individual confocal sections.

Analysis of incoming protein VI

HeLa cells (1.5 x 10^5) were seeded in a 12-well plate the day before the infection. HAdV-C5 (16.8μg) was added to the cells and allowed to bind and internalize at 37° C for 30min in RPMI 1640 medium supplemented with 0.2% bovine serum albumin and 20mM HEPES-NaOH, pH 7.4. Free virus was removed by washing the cells, cells were further incubated at 37°C for the indicated times in DMEM medium supplemented with 10% fetal calf serum, and thereafter lysed in lysis buffer (0.2ml of 200 mM Tris, pH 8.8, 20% glycerol, 5mM EDTA, 50mM DTT, 5% SDS, 0.02% bromophenol blue). Lysates were boiled at 95°C for 5min and centrifuged at 16,000xg for 5min. Proteins were resolved by SDS-PAGE and hexon and protein VI were detected by Western Blotting using anti-hexon (Abcam, ab6982) and anti-protein VI antibodies [26], and anti-β-tubulin (Amersham) as a loading control.

Electron microscopy

Cryo-ultramicrotomy and immunocytochemistry was performed based on the protocol of Tokuyasu [64] [65] [66]. The procedure was similar to one described earlier [26]. About 3x10^6 subconfluent cells were fixed in PBS containing 2% pFA and 0.2% glutaraldehyde for 1h, scraped off the dish, pelleted at about 500xg for 10min, washed several times in PBS, embedded in a small volume of 10% gelatine (Sigma, G6650) in PBS at 37°C, pelleted and solidified in a thin-walled Eppendorf tube on ice o/n. The cells embedded in gelatine were removed by slicing the tube wall, and infiltrated with 2.3M sucrose in PBS at 4°C for 2 days. The gelatine-cell block was mounted onto a metal plate, snap frozen in liquid nitrogen, and placed into a Leica EM Ultra Cut UC6 / FC6 machine. After trimming to about 0.25 mm^2 surface area, ultra-thin 80nm thick cryo-sections were obtained with a diamond knife at -120°C. Frozen sections were collected onto a drop of cold sucrose on a wire loop, brought to room temperature, and transferred from the loop onto a Formvar-coated Ni-EM grid (125μm mesh size). Grids were washed several times in PBS at room temperature, and at 40°C for 10min to remove the gelatine. Aldehydes were blocked by 3 short incubations in PBS containing 0.15% glycine, pH 7.5, and 2 washes in PBS. Samples were blocked in PBG buffer consisting of PBS, 0.2% gelatine, 0.5% BSA (AppliChem, A6588, 0050) and 0.01% Tween20 (Thermo Scientific, 28320) for 10min, and then with the primary rabbit immunoglobulin (IgG) anti-Gal3 antibody (PeproTech) at 1:20 in PBG for 1h

room temperature, washed 4 times 3min in PBG, blocked again for 3min, incubated with the secondary goat anti-rabbit IgG conjugated to 10nm gold (BBI Solutions) at 1:50 in PBG, washed several times in PBG, PBS, and H2O. Samples were fixed in 0.5% glutaraldehyde in H2O for 20min, washed 5 times in H2O, and stained in 1.8% methylcellulose, 0.3% uranyl acetate on ice for 5min. Excess liquid was blotted off, the sample dried on ice for several minutes, and analysed in a Philips CM100 (100kV at 46000 magnification using a digital CCD camera Gatan Orius 1000, 4kx2.6k pixels) or a ZEISS TEM10 (80 kV, 50000 magnification, using digital CCD camera Gatan Erlangshen ES500W, Model 782).

Citations

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